here (Figures 1, 2). They are apparently a generally biserial arrangement with indications of being slightly twisted. Such a development would place it in close relationship with *Siphogenerina* (*Sagrina* of numerous authors). In the megalospheric form figured by Brady, *Challenger*, pl. 76, fig. 17 (our figure 3), the early chambers are already apparently divided into chamberlets. In our specimens which show the early biserial stage, there are several chambers in a uniserial group which do not seem to be divided, and this character is only taken on after several simple ones are formed. As far as can be made out, the divisions of the chambers in *tessellata* are incomplete, but in some specimens they may be complete.

Our specimens show the apertural characters very well, and two of them are shown here. There is a definite neck with a spreading lip, as is characteristic of most species of *Siphogenerina*.

From a study of this series of specimens, it would seem that Silvestri's genus *Schubertia* may be used for *S. tessellata* (H. B. Brady) and *S. limbata* (H. B. Brady), but the structure of Brady's *Sagrina* (*?*) *annulata* is still in doubt. *Schubertia* is probably derived from *Siphogenerina* although it may be related to *Rectobolivina bifrons* which had numerous characters similar to those of *Schubertia limbata* particularly. The genus has existed in the Indo-Pacific region at least since the Early Tertiary, and today is widely distributed in that area from the coast of Africa to the Philippines and southward to Australia.

ZOOLOGY.—*Earthworms of North America.*[1] G. E. GATES, Judson College, Rangoon, Burma. (Communicated by MARY J. RATHBUN.)

Earthworms have received very little attention from our zoological investigators. Only one American, Frank Smith, has devoted any considerable amount of time to these animals, and his studies have been largely restricted to the species which occur in Illinois and contiguous states. It is to be expected that slimy creeping things which lack the beautiful colors of the moths and butterflies or the bizarre and curious forms of beetles and molluscs will not appeal to the instincts of the amateur collector, but an explanation for the neglect of such an important class of animals by professional zoologists is more difficult to find.

Several foreign zoologists have worked on American material, although, as a rule, they have been able to secure only small and quite

[1] Received July 22, 1929.

random collections. As a result of this situation any curious individual seeking information on the worms of this continent will find it necessary, in the absence of any comprehensive treatment of the subject, to wade through some ninety odd papers published in five languages in the scientific journals of eight different countries. In this mass of literature are records of occurrence in North America of 217 species of earthworms. Some few of the reports are mistaken, and a larger number of the generic and specific names are synonyms, but when these are eliminated enough remain to demonstrate that beneath the slimy, "repulsive," exterior is concealed a considerable variety of structure.

Structural variations, although of some interest, *per se*, become more significant when it is possible to distinguish primary from secondary characteristics and to arrange the various species thereby into a phylogenetic or evolutionary sequence. This has been done with some degree of success for earthworms, including many of the most characteristic genera of our own region.

Furthermore, although the number of species recorded from the area under consideration may seem at first thought to be rather large, it is probably but a fraction of the number of interesting forms that yet remain to be discovered. The records of distribution indicate how fragmentary our present knowledge is and at the same time suggest many opportunities for further investigation.

In the ensuing discussion earthworm is used to refer to any megadrilous oligochaete irrespective of terrestrial or aquatic habitat and North America is regarded as comprising not only all of the land mass north of the Panama Canal but also the islands of the West Indies.

The Acanthodrilinae

The ancestral type from which it is customary to trace many of the various lines of earthworm descent is known as the "Acanthodrilin Urform." This has the following characteristics:—

1. Paired testes and deferent duct funnels naked in segments ten and eleven.
2. The male ducts (vasa deferentia) on each side unite behind the second pair of funnels, pass backwards, and open to the exterior by a male pore on each side of segment eighteen.
3. Glands of unknown function called prostates, paired, tubular, and with an unbranched central canal open to the exterior on segments seventeen and nineteen.
4. Setae (solid, needle-shaped, chitinous bars embedded in epidermal sacs) four pairs per segment.

5. Nephridia (coiled tubular excretory structures) large, one pair in each segment. Loosely called meganephridia.
6. A single oesophageal gizzard located anteriorly in segments five, six, or seven.

Earthworms with the characteristics just enumerated are included in *Acanthodrilus*, a genus represented in our region by nine indigenous species. Six occur in Guatemala, one in Mexico, one in Cuba. One the distribution of which is either greater than the others or perhaps merely better known extends from Mexico to Guatemala. Elsewhere the genus is indigenous in South America, South Africa, Australia, New Zealand, and some of the Antarctic islands.

Microscolex was derived from *Acanthodrilus* by the disappearance of the posterior pair of prostates and the dislocation forward of the male pores to open to the exterior, together with the ducts of the anterior pair of prostates, on segment seventeen. This development of the male organs is known as the microscolecine reduction from the genus in which it was first observed, but it has appeared in other families as well as in the Acanthodrilinae. Two species of *Microscolex* have been found in various places on this continent but both are peregrine, i.e., widely distributed either by their own or by human effort and hence not of any zoogeographical significance. One of these species is the remarkable luminescent form *M. phosphoreus*.

In another genus of the family the anterior instead of the posterior prostates disappeared and the posterior pair of prostatic pores moved forward to open on segment eighteen near the apertures of the vasa deferentia. This genus, *Diplotrema*, is found today only in Queensland and New Caledonia, but from it was derived a large and important family, the Megascolecinae.

The Megascolecinae

The first genus of this family, *Plutellus*, arose from the Acanthodrilin *Diplotrema* by the fusion of the male pores with the prostatic pores on segment eighteen. This condition of the male apparatus remains characteristic throughout the whole family. The genus *Plutellus* was founded by Perrier in 1873 for a worm said to have been collected in Pennsylvania, but the species, *P. heteroporus*, has never again been found, in spite of the plea of Benham for the collection of further specimens. Six other American species have since been found, four in California, one in Guatemala, and one in Canada. This last, *P. perrieri*, from Queen Charlotte Island, has been collected but once, and is the only species of earthworm known to be endemic in Canadian territory.

Megascolides, the next genus in the Megascolecin line of descent, was derived from *Plutellus* by a "breaking up" of the nephridia, i.e., instead of one pair of "meganephridia" in each segment there may be three or four "micronephridia" on each side, all of the same size, or one on each side larger than the others. The single American species of this genus was found at Pullman, Washington, and described by Smith in a preliminary note in 1897. Although the worm is fairly large, 180–190 millimeters long with a diameter of six to seven millimeters, and in spite of the fact that the species was said to be very abundant in the region in which it was found, no further information has yet been made available. This may possibly be due to the fact that the burrows of this worm extend to a depth of over fifteen feet. Smith's specimens were obtained from a road cutting. Species of *Megascolides* are found elsewhere only in India, Australia, and Tasmania.

The next step in the evolution of the family was the branching of the central canal of the prostate. Worms with this development belong to the genus *Notoscolex* and occur in India, Australia, and New Zealand. From *Notoscolex* was derived *Megascolex* by an increase in the number of setae, at first to six or eight pairs, and then to a much larger number arranged in a more or less closed ring running completely around each segment. *Megascolex* is also limited to India, Australia, and New Zealand. Megascolecin evolution reached its culmination in the very large genus *Pheretima*, derived from *Megascolex* by a still greater increase in the number of setae per segment and the inclosure of the testes and male funnels within testis sacs. The genus is represented in North America by more than half a dozen species all of which are world wanderers. The peregrine forms of the genus are known to have been imported in dirt around the roots of plants into places far from their original habitat. This doubtless explains the finding of *P. hawayana* in the greenhouses in Evanston, Ill., and *P. heterochaeta* in greenhouses in Urbana, Ill. The occurrence of the latter species in fields of several Gulf States apparently indicates that accidental importation may result in permanent colonization.

The Diplocardiinae

A family much more characteristically American arose from the "Original Acanthodrilin" through the doubling of the gizzard, the initial genus, *Diplocardia*, having the Acanthodrilin arrangement of the male reproductive organs, lumbricin setae (four pairs per segment),

meganephridia, and two gizzards. This genus is remarkable for the variation in position of the male pores, these external male orifices being present typically on segment eighteen in only one species, *D. koebelei* from Morelos, Mexico. The male pores are on segment nineteen in *D. floridana* (Monticello, Fla.), *D. mississippiensis* (McNeill, Miss.), *D. michaelseni* and *D. udei* (Raleigh, N. C.), *D. longa* (Pulaski County, Ga.), *D. riparia* (Ill. and Ind.), *D. communis* (Ill.), *D. singularis* (Ill., Ind., and Raleigh), and *D. eiseni* (Fla., and Savannah, Ga.); on segment twenty in *D. verrucosa* (Ill., and Omaha, Neb.); and on segment twenty-one in *D. keyesi* (lower California and Chillicothe, Texas). As is evident from the preceding list which gives complete records of known distribution except for those species which have been found in two or more localities in a single state, much remains to be done in the way of working out the distribution of these typically American forms.

Zapotecia was derived from *Diplocardia* by an increase in the number of gizzards to three. Two species have been described, one from Mexico, the other from Haiti.

Trigaster was also derived from *Diplocardia* but by an increase in the number of nephridia per segment. Two species are known, one in Mexico, and one with three varieties in the little island of St. Thomas.

The culmination of the Diplocardin line of descent, so far as North America is concerned is *Dichogaster*, derived from *Trigaster* by the development of three pairs of calciferous glands in segments fifteen, sixteen, and seventeen. Three of the twenty-five species found in our region are either peregrine or of uncertain habitat, the other twenty-two have been obtained from Mexico (6), Costa Rica (6), Guatemala (2), Jamaica (4), Haiti (3), and St. Thomas (1). A portion of tropical Africa is characterized by the presence of a large number of species of endemic Dichogasters.

The Ocnerodrilinae

Another line of descent from the Acanthodrilinae was initiated by the development of paired oesophageal sacs in segment nine. *Kerria*, the most primitive genus of the family is represented in our fauna by three species, two in Lower California, and one in the island of St. Thomas. Numerous other species are found in South America.

Ocnerodrilus was derived from *Kerria* by the microscolecin reduction of the posterior male organs. Occasionally there are two pairs of prostates but when the second pair is present the prostatic glands

always open to the exterior on segment eighteen. *O. occidentalis* is the only representative of the genus in the United States but is peregrine and circummundane in the tropics. Sixteen endemic species are scattered through the southern portion of North America as follows: Mexico (7), Guatemala (7), Costa Rica (11), Cuba and St. Thomas (1).

Two other genera of the family come into our region with a single species each, *Gordiodrilus* with *G. dominicensis* in Dominica, and *Nematogenia* with *N. josephinae* in Costa Rica. Endemic species of both genera are found in Africa. The Ocnerodrilinae gave rise, apparently in Africa to another family, the Eudrilinae. A single species, *Eudrilus eugeniae*, has escaped from that continent and become widely distributed in the tropics, occurring in our continent in Panama and the West Indies.

Other Families

According to Michaelsen the Acanthodrilinae evolved from the Phreoryctinae, a group of small freshwater worms (Microdrili–Limicolae). Another line of descent from the Phreoryctinae resulted in the development of the other families which occur in our continent. The initial group in this second line of descent from the freshwater worms was the Glossoscolecinae which are characteristically South American but which come into our region with two endemic species of *Andiodrilus* in Costa Rica and two species of *Pontoscolex*. Other species of *Andiodrilus* are endemic in South America. Only two species of *Pontoscolex* are known; one, *P. corethrurus* which has been collected in Mexico and several Central American countries as well as in various islands of the West Indies, is pretty well scattered around the world in the tropics. A second species appears to be endemic in Guatemala. From some portion of the Glossoscolecinae there arose the Microchaetinae. This group of earthworms characterizes Africa except for a single genus in South America, *Drilocrius*, which intrudes into Costa Rica with one species. Another development from the Glossoscolecinae is the family Sparganophilinae of which only two species are known. One of these, *S. eiseni*, is widely distributed in the area from Guatemala to Michigan, but the other, *S. tamesis*, has been found only in the Thames River near Oxford, England, to which place it was presumably carried by man. The family is considered to be purely North American.

From the Microchaetinae by way of a very small, purely European

family, the Criodrilinae, Michaelsen derives the Lumbricinae, with endemic species in both Europe and the United States. From North America there have been collected 26 species of which eighteen are peregrine, presumably immigrants from Europe. Among this number are such well known forms as the nightwalker, *Lumbricus terrestris*, the dungworm, *Eisenia foetida*, and the very common *Helodrilus caliginosus*. All of the peregrine species have been collected more or less widely on this continent. Much less well known are the endemic forms. These include *Eisenia lönnbergi* described by Michaelsen who had specimens from Raleigh and Savannah, *E. carolinensis* founded by the same author for a single worm obtained from the dirt around the roots of a plant imported in the Botanical Gardens of Hamburg, Germany, from Fayetteville, N. C., and several species of *Bimastus*. There are no further records of the occurrence of *Eisenia* but the distribution of some of the *Bimastus* forms has been worked out more thoroughly. *B. palustris* has been collected in Pennsylvania, New Jersey, and in Raleigh, N. C.; *B. giesleri* in Savannah, Ga., Florida, Ohio, Illinois, Kansas, and Texas; *B. zeteki* in the Susquehanna River, N. Y., and in Douglas Lake, Mich., *B. tumidus* has been collected only in Mt. Lebanon, N. Y., *B. longicinctus* has been found only in Urbana, Ill. *B. welchi* was erected for a single specimen obtained in Manhattan, Kansas.

Zoogeographical Relationships

The occurrence of endemic species of the same genus in areas as widely separated as North America, Africa, India, Australia and New Zealand has of course attracted much attention from students of the earthworms. Interest in these problems has been increased by the demonstration that many of the purely terrestrial forms are limited in their movements by numerous natural barriers such as deserts, mountain-ranges and bodies of salt water. In the past it has been customary to regard the occurrence of these generically similar endemic species in widely separated areas as evidence for some sort of geographical connection between the areas concerned, in geological time more or less remote. Michaelsen even went so far as to maintain that in the Oligochaeta we have a group "which is capable of yielding results for paleogeography second to those of no other group in importance and certainty." The geographical relationships and their explanations so far as our own continent is concerned may be briefly summarized as follows.

Acanthodrilus is common to South America, South Africa, Australia and New Zealand. This distribution is taken as evidence for a former connection of the areas concerned either by a continuous Antarctic continent or by means of bridges represented today only by islands, the vestigial mountain tops of ranges that have sunk with the rest of the bridge beneath the sea. In a northward direction *Acanthodrilus* has penetrated into Central America presumably passing over the contemporary bridge connecting the two Americas, the Isthmus of Panama.

Plutellus and *Megascolides* originated in Australia or somewhere in the Australasian region and are supposed to have migrated into North America from Asia over a Behring bridge across the north Pacific.

In contrast to the Megascolecin forms, *Diplocardia* is thought to have originated in Mexico where it gave rise to forms that migrated northwards into the United States. Stephenson has described a species of *Diplocardia* from central India which, he assumes, reached that locality by migrating from North America over the Behring bridge in an opposite direction to that taken by the Megascolecin forms. Derivative genera such as *Dichogaster* are presumed to have wandered southwards and westwards to what later became the islands of the West Indies. The occurrence of numerous indigenous Diplocardin forms in Africa is regarded as evidence for a transatlantic bridge connecting Africa and Central America through the region of the West Indies. The Ocnerodrilinae furnish additional evidence for this Atlantic bridge.

Finally, the occurrence of endemic species of the Lumbricinae in South Europe and the United States is considered to be evidence for another bridge, probably in the North Atlantic region, connecting Europe and North America. The absence of endemic species of the family in the northern portions of both continents at the present time is explained to be the result of their extinction by glacial sheets of ice which covered these regions after the migration had taken place.

Bridges as explanations of earthworm distribution raise many difficulties, sometimes more than they obviate. Michaelsen has lately tried to avoid some of these difficulties by adopting Wegener's hypothesis of separation and eventual wide-apart displacement of continents from a single gigantic land mass. A diagram in Michaelsen's paper shows the southern portion of South America (*Acanthodrilus* region) in contact with the southern portion of Africa, the

Diplocardia region of Central America continuous with a central African *Dichogaster* belt, and the endemic *Eisenia* region of the United States in contact with a corresponding area in southern Europe. According to this theory, the worms concerned migrated from one region to another while the land masses were still in contact, then later on a separation and pulling apart of the continents brought about the formation of the deep ocean basins between.

More recently still Stephenson has pointed out certain indications tending to show that the earthworms are a relatively recent group, much more recent in fact than the gigantic land mass of Wegener or many of the bridges invoked to explain the facts of their distribution. In place of bridges Stephenson offers as his contributions to a solution of the problem transportation of cocoons in mud on the feet of birds, transference of adult forms in natural rafts, and polyphyletic origin of some of the genera concerned, i.e., the origin of a genus independently from different species of the same ancestral genus or even from two or more different genera.

The cocoons of earthworms, however, are usually deposited, by the purely terrestrial forms at a depth where there is very little likelihood of their becoming entangled in mud on the feet of birds, and furthermore, being rather slippery may be expected to offer considerable difficulties in the way of long distance transportation by birds. Raft transference of adult worms does not seem to be of much value in explaining the passage of worms between continents widely separated by permanently deep ocean basins. Finally it does not seem too much to expect at the present, that further study will enable the separation of mixed groups into genera of purely monophyletic origin, for the vast majority of our present species are based upon characteristics visible in dissection without adequate knowledge of the microscopical anatomy. Little or nothing at all is known of the oligochaete fauna of many large and very important areas and the thorough exploration of these regions together with detailed microscopic studies may be expected to assist materially in the solving of problems of the evolution and distribution of the earthworms.